Natural Selection: Deriving Causality from Equilibrium

Long Abstract

Natural selection is often represented as one of the main causal mechanisms driving evolution, and is often modeled in biology textbooks as some kind of Newtonian force, with magnitude and direction. However, this picture is complicated when one takes into consideration how evolution by natural selection is constituted by individual births and deaths. Following a number of articles by Walsh, Ariew and Matthen, there is now a significant challenge that natural selection may not even be a cause, let alone a Newtonian force. Individual births and deaths can be described independently of natural selection. Natural selection is no causal propensity over and above individual-level processes; rather, it is a statistical effect, a mere book-keeping of the genuinely causal interactions that take place between individual organisms (Matthen and Ariew 2009; Walsh, Lewens and Ariew 2002; Walsh 2007).

In the extensive literature that has ensued, the statisticalist approach has mainly been used to argue for a *deflationary* position "fitness and natural selection have no reality except as accumulations of more fundamental events" (Matthen and Ariew 2002, 82). In this paper I will to investigate the underexplored possibility of a non-deflationary statisticalist analysis of selection. This adopts the statisticalist, bottom-up analysis of population change, but tries to reconcile it with certain causalist intuitions. The inspiration for this is that, while statisticalist considerations may preclude certain naïve ways of understanding the causal nature of selection, causalist intuitions cannot be entirely wrong either. At the very least, it cannot be denied that most of biological practise is not threatened by these considerations. While it may be metaphysically inacccurate, it is often empirically accurate to model selection as a causal force (for example in cases of stabilizing selection, where component pressures cancel out). This suggests that causalist intuitions must be legitimate in some way.

My approach in this paper will be to use the notion of *equilibrium* as a way of understanding how the causal nature of selection can be real, thus grounding causalist intuitions. Equilibrium is a central concept in modeling the behavior of complex systems. In particular, stable equilibria are empirically important because they act as attractors and allow for a long-term prediction of the behavior of the system, even though the behavior in the middle-term may be chaotic and too complex to calculate. However, they are also philosophically important as they can allow a well-defined *direction* to be assigned to a complex process. Thus a concept of directionality can be formulated that is grounded in a statistics of individual-level dynamics and that allows us to understand why natural selection can be legitimately called causal.

To establish such a framework, I will need to do three things. The first task will be to lay the ground by disentangling some different notions of causality at play, in particular process and difference-making causality. Each highlights a different aspect of natural selection and confusion results if these are not kept separate. In this paper I will focus on difference-making causality alone, mainly because this notion has been more controversial. Difference-making is, broadly, counterfactual dependence. The statisticalist arguments have endeavored to show that, even if natural selection were not present, evolutionary change would occur.

One argument has been that natural selection is established only retroactively, by a statistical regression on actually occurred births and deaths (where selection is the correlation between traits and births). There is no description-independent way of establishing fitness or natural selection (and this is related to the reference class problem). Another argument has concerned the inseparability of natural selection from the causal processes affecting the behavior of organisms. The probabilities that characterize the possible outcomes by natural selection are only a measure of our ignorance of the individual-level processes determining the births and deaths. They do not correspond to any putative 'causal propensity' that could be used to ground natural selection.

The second task will be to formulate the condition of equilibrium, and to show how, if it is accepted, it can resolve certain key issues regarding difference-making causality. For this I will use an extension of the Price equation to the multigenerational case. The Price equation gives an exact relationship between the phenotype distribution of different generations:

$$\overline{z}^{(k+1)} - \overline{z}^{(k)} = Cov(\omega^{(k)}, z^{(k+1)}) + E[z^{(k+1)} - z^{(k)}],$$

where $z^{(k)}$ is the phenotype variable of the kth generation, $Cov(\omega^{(k)}, z^{(k+1)})$ a measure for how relative fitness ω covaries with phenotype z, and $E[z^{(k+1)} - z^{(k)}]$ the expected transmission bias. I will show how this equation can be simplified considerably under assumption that an equilibrium is reached after a certain number of generations. This assumption then allows one to uniquely define a direction of an evolutionary process: the tendency towards equilibrium.

This is important because it allows one to argue that the probabilities defining fitness are not purely description-dependent. Neither is natural selection merely a measure of subjective uncertainty; rather, it reveals an objective feature of certain evolutionary processes, namely the presence of stable equilibrium. Natural selection is causal in the difference-making sense: if it were not present, an evolution towards stable equilibrium would not be observed.

Finally I will need to argue why the equilibrium condition is a plausible assumption. To this end, I will show that given evolutionary change, either a stable equilibrium is reached, or if it is not, then the concept of fitness is not meaningful. I discuss certain results from Markov process literature, where the conditions for equilibrium are established (Doeblin's theorem). From this it can be seen that the notion of equilibrium is intertwined with natural selection, and that this is a natural way to reconcile both statisticalist and causalist approaches.

Length: 930 words